Sociobiology 63(2): 744-747 (June, 2016) DOI: 10.13102/sociobiology.v63i2.848

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - ANTS

Trophic Ecology of the Ant *Pachycondyla crassinoda* (Formicidae: Ponerinae) in a Lowland Neotropical Forest

AE Tudor, CK Starr, K Mohammed

University of the West Indies, St Augustine, Trinidad & Tobago

Article History

Edited by
Gilberto M. M. Santos, UEFS, Brazil
Received 14 June 2015
Initial acceptance 11 August 2015
Final acceptance 10 April 2016
Publication date 15 July 2016

Keywords
Tandem running, foraging, predation.

Corresponding author
Christopher K. Starr
Dep't of Life Sciences
University of the West Indies
St Augustine, Trinidad & Tobago
E-Mail: ckstarr@gmail.com

Abstract

Pachycondyla crassinoda (Latr, 1902) is one of the largest ant species in the New World tropics with a worker body length of about 18 mm. We studied its foraging habits in the field in a lowland forest in Trinidad, West Indies, with supplemental observations in the laboratory. The estimated density of colonies at our study site, 144/ha, is probably exceptionally high for this species. Like other members of its genus, *P. crassinoda* forages on the forest floor, apparently never climbing trees or other plants. Foraging is mostly limited to periods when the ground is relatively dry and is largely close to the nest. Ants searched under fallen leaves at a high frequency and preyed mostly on small arthropods. They seldom stung prey, never unless the prey struggled vigorously. The only form of food-source recruitment observed was tandem running, with a maximum of two nestmates following the scout.

Introduction

Ants are the main predators of land invertebrates in most of the world, withwide variation in foraging habits and the degree to which these are specialized (Hölldobler & Wilson, 1990; Lach et al., 2010; Traniello, 1989). Initial scouting for food sources is most commonly by separate individuals, but in many species a scout who finds a good source then recruits nestmates to aid in its exploitation. In some species large food items are typically retrieved by several nestmates. Food-source recruitment, where it exists, can take several forms, including tandem running (a nestmate follows the scout closely back to the food source, maintaining constant physical contact) and laying odor trails. The latter method can be extremely efficient, quickly bringing a large mass of nestmates to the food source and potentially allowing the colony to monopolize it.

Pachycondyla is a largepantropical genus of ponerine ants. *P. crassinoda* (Latr, 1802) is the largest member of its genus in the New World, the robust, all-black workers having a body length of almost 20 mm (MacKay & MacKay, 2010). It is the second largest of all ants (after *Paraponera clavata* Fabr.) in much of its broad range in South America east of the Andes and north of the Southern Cone, while in Trinidad it is the largest. It nests in the soil, typically under rotting logs or between tree roots (Henriques & Moutinho, 1994). The workers are commonly encountered on the surface of lowland forests. Our preliminary observations indicated that foragers very often briefly looked under fallen leaves on the forest floor and that if disturbed they typically hid under leaves. The workers' sting is initially sharp and painful, fading within a few minutes (pers. obs. of CKS).

For such a conspicuous, widely distributed species, *P. crassinoda* has been surprisingly little studied. In the main study to date, based on three laboratory colonies, Henriques and Moutinho (1994) reported very small colony sizes, a simple nest structure and social organization similar to that of other studied *Pachycondyla* species, and food-source recruitment by tandem running. They concluded that the 33 behavior patterns recorded from workers were probably close to the complete repertory. Silveira-Costa and Moutinho (1993) described the behavior of nestmate recognition in *P. crassinoda*.

ISSN: 0361-6525

Our purpose here is to describe the foraging habits of *P. crassinoda* with a view to understanding its place in the ecosystem. Given its very large size and powerful stinger, we hypothesized that it preys mainly on unusually large invertebrates beyond what other sympatric ant species can subdue.

Materials and Methods

All field study was at the Arena Forest Reserve (10°34'N 61°14'W) in northeastern Trinidad, West Indies.The soil is sandy and well drained, with an undulating surface fragmented by many streams. The well-developed secondary forest has a closed canopy. As in the rest of Trinidad, there is a moderately pronounced dry season from about mid-January to the end of May. Our field observations, amounting to about 200 person-hours, were from September 2012 to January 2013, and September 2014 to January 2015. Laboratory observations were from November 2014 to March 2015. Preliminary observations suggested that foraging activity (measured as number of workers seen on the forest floor) is greatest during the warmest part of the day from late morning to early afternoon. Accordingly, our field observations were conducted from about 09:00 to about 12:00. Preliminary observations likewise suggested that foraging activity is sharply reduced during and soon after rain.

The study area was mapped with the aid of measuring tape, compass and flagging tape. It comprised 0.325 ha bounded by two broad trails and a stream (Fig 1). Within this area was a small, shallow pooland a small, low peninsula (marked "floodplain") that was flooded when the stream was exceptionally high.

Our principle method in locating colonies was by laying out baits (fragments of cooked pork fat) throughout the study site and following foragers back to their nests (Agosti et al., 2000), which we then marked with numbered stakes. We continued this for several weeks until very few of the nests we were finding were novel. A few nests also came to our attention by the typical tumulus of excavated soil at the entrance. Baiting also allowed us to observe recruitment and retrieval of food items.We spent a significant minority of field time observing the behaviour of workers outside of the study site.

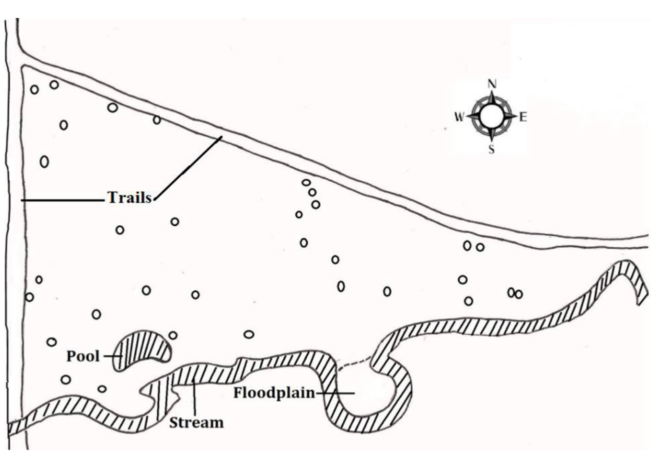

Fig 1. Study area in the Arena Forest Reserve at 10°34'41"N 61°14'35"W. Circles indicate sites of known *Pachycondyla crassinoda* nests. Several of theseeach represent two apparently distinct colonies very close to each other.

In order to study how ground moisture affects foraging activity when not raining, one of us (AET) undertook paired walking transects at about 09:00 and 11:00. Each transect followed a standard route for 30 min at a moderate walking pace, enumerating the workers on the trail or within about half a meter of its edge. These were done under three conditions: a) ground mostly dry, b) much of the ground moist with no significant standing water, and c) ground mostly wet with many spots of standing water.

In order to determine whether foragers search over a wide area, we followed individuals for a total of 10 min each, estimating to the nearest meter the distance between their positions at the beginning and end of the period. At the same time, we counted the number of fallen leaves under which the worker at least put her head during the 10 min.

We studied food preferences in the field by means of a simple cafeteria experiment. Five kinds of food (moistened sugar, finely-chopped fresh fruit, crumbled salt crackers, ground cooked meat, and freshly-killed grasshopper) were placed on a dry fallen leaf within a meter of at least one nest on three relatively dry days. We then recorded instances of retrieval from the cafeteria.

We collected five colonies for laboratory observation, beginning by collecting ants coming to baits placed near the nest entrance until very few new ones appeared, and then excavating. We failed to find the queen of three colonies, although collection appeared to be close to complete.The queenless colonies continued in apparent good health for several weeks. We provided laboratory colonies with a variety of live arthropods (grasshoppers, cockroaches, termites, beetles, large ants) similar to those found on the forest floor and whole or fragmented earthworms. These were categorized into three size classes: a) large (about the size of a worker ant, n=136), b) medium (about the size of an ant's head, n=288), and c) small (distinctly smaller than the head, n=112).

Results

Within the study area we identified 48 colonies in the study site, presumably not far short of the true total. Without attempting a dispersion analysis, the appearance is of a modest degree of clumping (Fig 1), presumably due to unevenly suitable substrate. Not only were there no colonies on the floodplain but we never observed a forager there.The six colonies that we were able to census apparently nearly completely had between 52 and 86 known workers.

In our many hours of observing workers in unhindered activity outside the nest, we never saw any individual climbing a tree trunk or other plant. All indications are that foraging activity is strictly at the soil surface.

The transectstudy recorded 112 foragers during two pairs of dry-condition transects, versus 12 during one pair of moist transects and nine during two pairs of wet transects.

Of the 20 workers whose movements were monitored for 10 min, 12 (60%) were one meter from the starting point at the end of observation. Seven of the others showed a net displacement of either zero or two meters, and one ant was six meters away. The search pathway did not give the impression of being a random walk, as there was a great deal of turning back, and it was not uncommon to see an ant walk over the very same spot more than once during monitoring. The total distance traveled in each case was evidently several times the net displacement.

The 20 ants searched under a mean of 27.3 (range 12-46) fallen leaves in the course of 10 min. On two occasions we observed an ant returning from under a leaf with a small prey in her mandibles and proceeding directly away in the manner as ants returning to the nest with baits. There is, then, striking difference between a worker scouting for food and one retrieving.

We observed 21 instances of tandem running, mostly to baits. Of these, 17 involved two ants; the other four involved three ants. On the other hand, we never observed two or more ants in group retrieval of a food item, despite ample opportunity if this does occur. Most baits were at least the size of a worker ant when first laid out, and if too large for a single ant to carry she would chew off a smaller piece.

Given the overall density of nests, it was to be expected that foragers from different colonies often contact each other. Workers from different colonies often appeared at the same baits, commonly coming into direct contact. In no case did we observe any apparent antagonism or attempt to repel other workers. However, they were antagonistic to the social wasps (*Angiopolybia pallens* (Lep.)) that frequently came to baits.

The cafeteria experiment yielded 24 observations of retrieval. Of these, 21 were of grasshoppers or fragments of grasshoppers, the other three of cooked meat. That is, they spurned the fresh fruit, salt cracker, and even concentrated sugar solution. On the one occasion we found that the baits we had brought to the field showed evident decay (judge by smell). The ants accepted these apparently as readily as they did freshly-cooked bait.

We recorded just 12 preys in the field. Insofar as they could be identified, these were a variety of immature and adult arthropods. One was roughly the same size as the ant, the others much smaller, roughly the size of the ant's head.In the laboratory we recorded no instance of a forager stinging a medium or small prey, and they stung large prey only when these struggled vigorously. In several cases, two or more workers attacked and stung an especially difficult large prey before cutting it into pieces for individual retrieval.

On one occasion in the field we observed several ants at three open wild nutmeg (*Virola surinamensis*) (Myristaceae) fruits that had fallen to the ground. They were collecting and transporting fragments of the bright red ariloid.

Discussion

The known density of colonies in the study area was 144/ha. Because the study site was chosen for its apparent wealth of *P. crassinoda* foragers, this is probably close to the maximum density for the species, at least toward the northern end of its range.

Foraging at the ground level only is typical of *Pachycondyla* (J.T. Longino, pers. comm.). Differences in number of foragers observed on transects during differing ground conditions are striking enough that no sophisticated statistical analysis is needed. The ants are clearly more active when the ground is drier (χ^2 test, $p<0.01$).

It is known that *P. crassinoda* workers distinguish nestmates from other conspecifics (Silveira-Costa & Moutinho, 1993), so that the lack of antagonism between non-nestmates at large, valuable baits is notable.

Given a choice of food, it prefers live or freshly-killed arthropod prey without specializing, although it also takes carrion and vegetable matter on occasion. Against our working hypothesis, *P. crassinoda* appears to prey mostly on animals just a fraction its own size and seldom stings them. The ariloids of *Virola surinamensis* appear to have a strikingly high lipid content (Horvitz, 1981; Maya et al., 2006). This, along with the ants' strong foraging at cooked pork fat, suggest that the ants normally have little access to lipids. A tendency not to sting prey is consistent with the hypothesis that venom is metabolically expensive and best reserved for defense of the colony or self-defense against large predators.

The picture emerging from our observations is of an ant that searches solitarily close to the nest and mostly under fallen leaves for small prey, avoiding wet ground conditions, with little recruitment of nestmates.

Acknowledgements

We thank Luke Rostant and Lee Ann Beddoe for assistance with various aspects of this project, and these and Alda Henriques, Jack Longino, Danielle Morong and the journal's reviewer for helpful comments. Rakesh Bhukal provided very valuable field assistance.

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